7 Nutrient interactions of detritus and decomposers

7.1 INTRODUCTION

In nearly all ecosystems, the majority of primary production is not consumed by herbivores, but passes directly to dead organic matter, or detritus. A smaller fraction of primary production is incorporated into herbivores and carnivores, which becomes detritus when these organisms die. The decomposition of dead organic matter is carried out by a diverse collection of organisms, ranging from microorganisms (fungi and bacteria) to relatively large animals (earthworms and millipedes). These, in turn, support an array of predators that obtain their sustenance wholly or largely from energy and nutrients stored in detritus.

Energetically, the food web based on detritus in an ecosystem may be more important than the food web based directly on autotrophic production (the grazing chain). For example, W. E. Odum (1970) worked out a food chain based on fallen mangrove leaves in southern Florida. Only about 5% of the leaves were grazed (primarily by insects) while they were alive. Fungi and bacteria colonized the dead leaves that fell in the water and a diverse group of detritivores then fed on the leaf particles and their microbial communities. These detritivores included insect larvae, nematodes, harpacticoid copepods, amphipods, crabs, snails and sheepshead minnows. As E. P. Odum (1971) pointed out, the energy that passed through the mangrove detrital food web may make a substantial contribution to the coastal fishery of southern Florida.

In addition to its importance as an energy source, detritus serves as a reservoir of nutrients. Decomposers regenerate these nutrients, so that they become available again to autotrophs. In terrestrial ecosystems nutrients released in mineral form by weathering are 'generally insignificant in relation to the nutrient demand of the vegetation. The major part of the nutrient replenishment is accomplished by the mineralization of the elements by the action of decomposer organisms. *Mineralization* is the conversion of an element from organic to inorganic form' (Swift *et al.*, 1979). Aquatic ecosystems also rely heavily on mineralization of nutrients (or remineralization if the nutrients were originally in inorganic form), particularly the phosphorus bound in phytoplankton and macrophytes. For example, Carpenter (1980) showed that the release of phosphorus from

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decaying submersed macrophytes may be a stimulus to pelagic primary production in lakes. In a phytoplankton culture studied by DePinto *et al.* (1986), phosphorus regeneration rates were less than 0.01 d^{-1} in cultures not inoculated with a decomposer community, but were two to five times higher for decomposer-inoculated cultures.

The purpose of this chapter is to consider the various roles detritus and the decomposer food web play in the dynamics of food webs. The size of the detritus component and the pool and nutrients held by it, controlled in part by the decomposition rate, has an important influence on food web stability. The details of the detrital/decomposer interactions also have other, more complex effects within the ecosystem.

Up to this point, the dead organic matter or detritus of an ecological system has been considered to be only a pool from which nutrients are released at a constant rate back to the pool of nutrients available for uptake by autotrophs. This simplified view overlooks the nature of detritus as a system of complex activity that is important in its own right. In this complex detrital subsystem, the return of nutrients to the available pool is not nearly as simple as described by the constant rate coefficient, d_D, used in earlier chapters. This chapter adds some complexities and explores their implications for the dynamics of food webs. This will require a more detailed description of the process of decomposition, including the explicit modelling of the decomposers and, in some cases, the heterotrophs that feed on these decomposers. Before pursuing this increase in model complexity, we will first examine, with models developed in earlier chapters, the importance of the size and turnover rate of the detrital compartment to the stability of the food web.

7.2 EFFECTS OF DETRITUS COMPARTMENT SIZE ON AUTOTROPH–HERBIVORE STABILITY

A large detrital component will usually have the effect of lowering variability of available nutrients in the ecosystem. Fluctuations in the nutrient input rates and loss rates can be buffered by nutrient releases from the large reservoir in the detrital biomass so that primary production is less variable. In view of this, it would seem that a system with a large detrital biomass component would usually be more stable than a system that has a small detrital biomass, though equivalent in other respects.

Paradoxically, model simulations show that systems with large detrital components may be associated with a greater tendency towards oscillatory behaviour than systems with small detrital components. Limit cycle oscillations are the result of local instability of a system, which was explored with respect to autotroph–herbivore interactions in Chapter 5 [Equations (5.16)]. In the analysis in Chapter 5 it was noted that local instability can result

from nutrient enrichment, Rosenzweig's (1971) 'paradox of enrichment'. In systems with a large nutrient input, autotroph–herbivore interactions are more likely to produce instability and limit cycle oscillations. Thus, a reduction in nutrient input, I_n, tends to reduce oscillations in model ecosystems. When nutrient is limiting, irruptions in autotroph biomass are opposed by a decrease in the concentration of limiting nutrient. If this reactive decrease is sufficiently strong, the autotroph–herbivore oscillations may be damped.

The greater vulnerability to autotroph–herbivore limit cycles of models with large detrital components is probably due to the fact that the detritus releases nutrients into the available nutrient pool, N. This is at a rate in which N is maintained at a higher average level in this case than when the detrital component is small. The higher level of available nutrient would favour the autotroph–herbivore instability.

This proposed mechanism was tested through model simulations of hypothetical systems with small and large detrital components. The dynamics of the four variables: available nutrient, N, autotroph biomass, X, herbivore biomass, Y, and detritus, D [described by Equations (5.16)] are shown in Figure 7.1(*a*,*b*) for two values of the detrital loss rate, e_D; 1.0 and

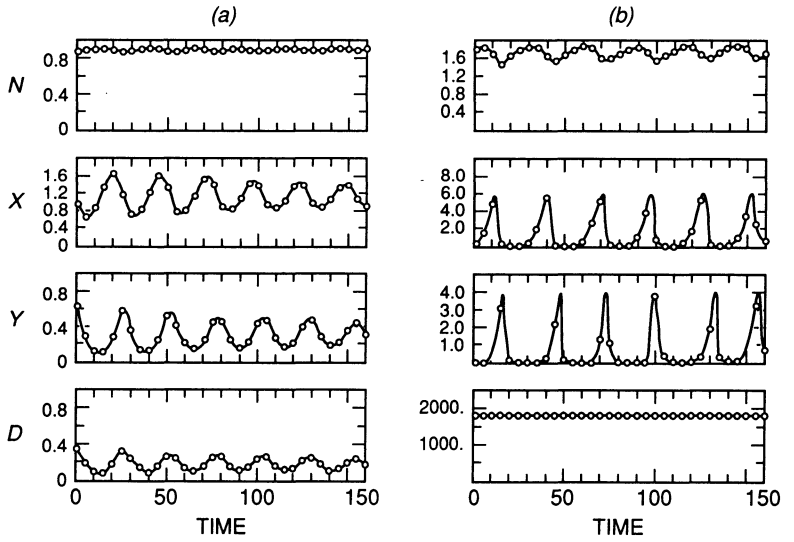

Figure 7.1 Simulations of available nutrients (N), autotroph biomass (X), herbivore biomass (Y) and detrital biomass (D) for a hypothetical system described in Equations (5.16). (*a*) Low detrital biomass, $e_D = 1.0$; (*b*) high detrital biomass, $e_D = 0.0002$. Other parameter values are: $I_n = 0.01$, $r_n = 0.001$, $k_1 = 10$, $k_2 = 10$, $d_1 = 0.06$, $d_2 = 0.5$, $e_1 = 0.0001$, $e_2 = 0.0$, $f = 5.0$ and $\eta = 1.0$, $g_1 = 0.02$, $r_1 = 2.0$, $d_D = 0.0001$, $\gamma = 0.05$. (Units are arbitrary.)

0.0002, associated with loss of nutrient from the system. Other parameter values are listed in the figure caption. Detritus was lost from the system at a higher rate in the first case than the second, so that recycling to the available nutrient pool was lower in the former case.

In the case with $e_D = 1.0$, the detrital component was small and varied as a result of the autotroph–herbivore oscillations, but these oscillations slowly damped out [Figure 7.1(*a*)]; whereas, when $e_D = 0.0002$, the detrital component was large and stable, but there appeared to be autotroph–herbivore limit cycle behaviour [Figure 7.1(*b*)]. The intense oscillations in the second case are caused by the fact that the average level of available nutrient is higher due to the larger detrital accumulation and larger fraction of nutrient recycled through the detritus.

7.3 EFFECTS OF DETRITUS COMPARTMENT SIZE ON RESILIENCE

In the preceding section, a system was examined in which autotroph–herbivore interactions are likely to lead to instability and oscillations. It was shown that a large, constant detrital reservoir of nutrients made it less likely that these oscillations would be damped by out-of-phase oscillations in available nutrients.

Let us now shift attention towards ecosystem models that are locally stable and not vulnerable to oscillations. For these systems, the resilience, or rate of return to steady-state equilibrium following a perturbation, is a key property in characterizing system dynamics. Detrital biomass plays a special role with regard to the resilience. Dudzik *et al.* (1975) performed detailed simulations of two abstract models: one a model of a shallow, mesotrophic freshwater lake and one of a grassland ecosystem. These were modelled with different levels of detail, ranging from four to eleven components (Figure 7.2). Organic litter or detritus was a component in each of these systems. One of the key generalizations Dudzik *et al.* derived from a study of their models was that: 'Perturbations in the organic litter pool can lead to more severe disturbances of the ecosystem, than the same-sized perturbations in other compartments.' In fact, in simulations of the grassland ecosystems, plant cover diminished by 50% following a 10% reduction in organic litter, and decomposers also underwent a drastic decrease. Even after a 20-year simulation, there was only a slight recovery from disturbance.

There is a logical explanation for the importance of detritus and disturbances to this component. In each of the models studied by Dudzik *et al.* (1975), organic detritus was by far the most massive compartment, holding a large fraction of the nutrient in the system. A removal of 10% of the detrital biomass in such a system, especially in a low-subsidy system where primary production relies on nutrients recycled from the detritus rather than external inputs of nutrients, can have a long-term disruptive effect.

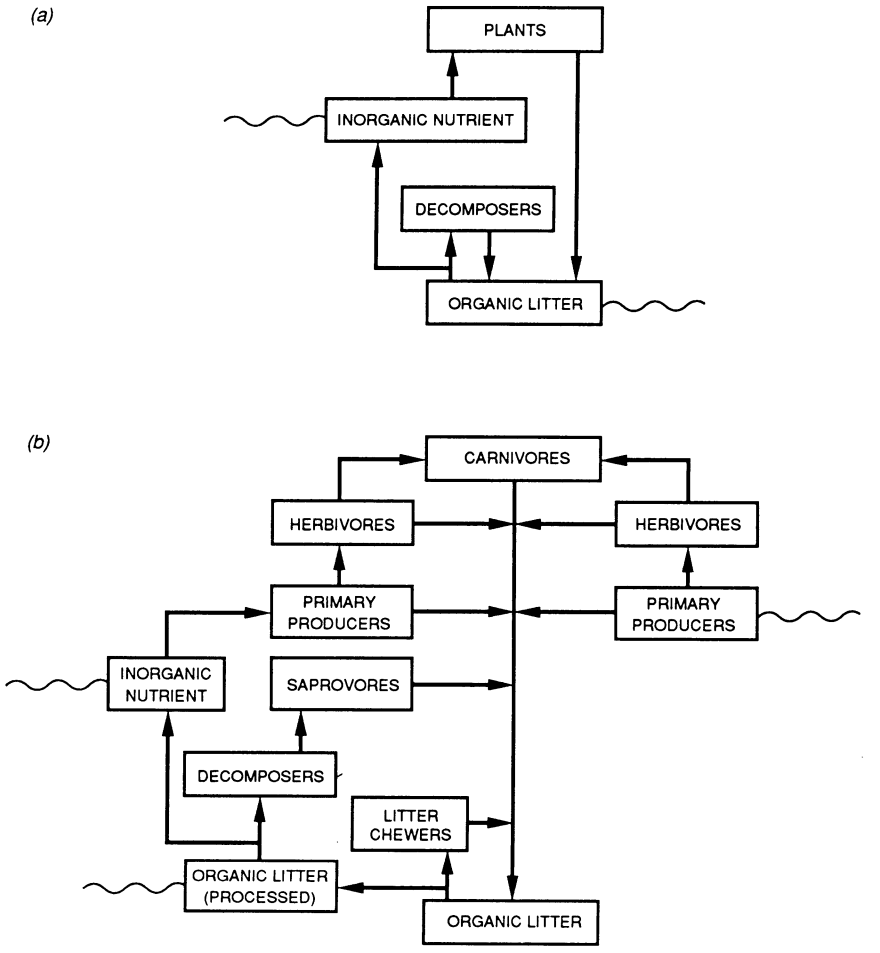

Figure 7.2 General models of nutrient cycling analysed by Dudzik *et al.* (1975). (*a*) Simple model and (*b*) complex model.

A simple model can be used to help interpret these results and to provide some general understanding of how the resilience of a system can be influenced by both the size of the detritus compartment and the nature of the disturbance. The model used is the same as in the preceding section [Equations (5.16)], except that the interaction term between the autotrophs and herbivores is changed from a Holling Type II interaction to a Holling Type III. The use of the Holling Type III function helps stabilize the system to ensure that it will return to equilibrium following a perturbation. Two widely different rates of detrital decomposition are assumed ($d_D = 0.1$ for one case and $d_D = 0.0001$ for another) so that steady-state detrital compartments of different sizes are established for the two cases. Two different types

of perturbations are also applied to the system: (1) A perturbation that removes an amount (10%) only from the available nutrient N, autotroph X and herbivore Y components and (2) a perturbation that removes 10% from each of the four components. Thus, there are four different treatments. These are used in simulations to determine the effects on resilience, or inverse of the return time to equilibrium.

The return time to equilibrium, T_R [return to a fraction $e^{-1} = 0.37$ of the original displacement, averaged over the compartments as in Equation (2.8)] was calculated for each of these cases. The results are shown in Table 7.1. On the one hand, when the detritus compartment is small ($d_D = 0.1$, so the amount of nutrient it stores is of the same order as the nutrient in the other compartments), the return time to equilibrium is about the same whether only N, X and Y are perturbed or N, X, Y and D are all perturbed. On the other hand, when the detrital compartment is large ($d_D = 0.0001$), so that it stores a much greater amount of nutrient than the other components in steady state, the behaviour following a disturbance differs depending on whether the perturbation affects the detritus or not.

The above results have a simple intuitive explanation. When the detrital component was very large, a large fraction of nutrient in the system was tied up in that compartment. A decrease of 10% in the other, smaller compartments had little effect on the total nutrient in the model ecosystem. In fact, following the perturbation to the autotroph, herbivore and available nutrient components, the detrital compartment remained roughly constant. Since most of the nutrient used by the autotroph came to it via recycling from the detritus, the autotroph production continued roughly at its steady-state rate, and recovery was rapid (i.e. high resilience). When the large detrital component was perturbed by a removal of 10% of the organic matter, this caused a substantial depletion of the total nutrient in the whole system. None of the components returned to their former values until the external nutrient input had restored sufficient limiting nutrient to the system. The time required was roughly equal to the turnover time of the limiting nutrient

Table 7.1 Return times to steady-state equilibrium, T_R, following a perturbation for the system of Equations (5.16) (with Holling Type III interactions between autotrophs and herbivores) for two different detrital biomasses; corresponding to decomposition rates $d_D = 0.1$ (corresponding to small detrital biomass) and 0.0001 (large detrital biomass) and for two types of perturbations; one affecting all components and one affecting all but detrital components. The units here are arbitrary

	Decomposition rate	
	0.1	0.0001
Perturbation of N, X, Y	834.6	395.4
Perturbation of N, X, Y, D	876.4	1944.0

in the whole system. When the detrital compartment was small, a perturbation of the autotroph, herbivore and available nutrient removed a considerable fraction of the nutrient and the recovery rate of these components was limited by the relatively low input of external nutrient subsidy. The difference in results for the perturbed compartments between systems that have high and low decomposition rates can be interpreted in terms of the nutrient turnover time, $T_{res} = N^{\ddagger}_{\dagger}/I_n$, of the system (where $N^{\ddagger}_{\dagger}$ is the total amount of nutrient stored in the system at steady state and I_n is the rate of nutrient input). The turnover time is greater in the system with the low decomposition rate, because a large amount of nutrient is stored in organic matter in this case.

The above analysis supports the results of Dudzik *et al.* (1975) concerning the importance of perturbations to organic litter detritus when this component contains the bulk of nutrients in the system. As can be expected by analogy, when other components of the system act as the primary storage reservoirs of nutrients in ecosystem models, the system is most sensitive to perturbations that remove fractions of those components. Dudzik *et al.* (1975), for example, showed that a model of a tropical rain forest had least resilience to perturbations that removed a fraction of autotroph biomass, since a large proportion of nutrients was stored in the woody parts of trees.

7.4 INFLUENCE OF DECOMPOSERS ON NUTRIENT RECYCLING

The simple models of earlier chapters assume not only that detritus or litter decomposes at a constant rate, but that other nutrients are released from the detritus at the same rate that the biomass decomposes and releases its main component, carbon; that is, the carbon/nutrient ratio remains constant through time. This assumption has been demonstrated to be false for many systems.

The difficulty with the assumption of constant carbon/nutrient ratio is that the activities of decomposers are themselves dependent on the ratios of nutrients in detritus and available nutrients in inorganic form. Because decomposers require nutrients, they can, when detrital nutrient concentration is low enough, act as a net sink for available nutrients in the system rather than as a net source.

Aber and Melillo (1975) found that the concentration of nitrogen in many forest litter types increases linearly as the detritus undergoes weight loss and that this trend can continue until a large fraction (at least 50 to 60%) of the original weight has been lost. This finding has been corroborated for many systems: N in floodplain and upland forests (Peterson and Rolfe, 1982; Kelly and Beauchamp, 1987); N and P in freshwater emergent macrophyte litter (Morris and Lajtha, 1986); Ca, Mg, N, P and K in plant litter in bush-fallow in sub-humid tropical Nigeria (Swift *et al.*, 1981); N in *Spartina alterniflora* litter in salt marshes (Marinucci *et al.*, 1983); N in pine litter (Berg and

Ekbohm, 1983); and P in slash pine litter in northern Florida (Gholz *et al.*, 1985). Large decaying boles in forests are often sinks for nutrient elements because of their high ratios of carbon to other nutrients. In an old undisturbed forest these boles were shown to make up 9% of the detritus (Lang and Forman, 1978). In addition to this increase in nutrient concentration in litter through time, litter has been found to decompose more rapidly when nutrients are added (e.g. Anderson, 1978).

The phenomenon of increasing nutrient concentration in litter has been explained to result from the *immobilization* of inorganic nitrogen from water solution during the microbial decomposition of the organic carbon of litter with high carbon/nutrient ratios. In this process a net gain in organic nitrogen in litter occurs (decomposers die and become part of the litter) and at the same time a net loss in organic carbon results from CO_2 evolution. The result is a decrease in the organic carbon/nutrient ratio. In this explanation, the 'organic matter' includes both the substrate for decomposition and the decomposer organisms. Addition of nutrient speeds up decomposition because the decomposers are nutrient limited.

In contrast to the decrease in the carbon/nitrogen ratio in litter when this ratio is initially high, it has been found that decomposition or organic matter with low carbon/nitrogen ratios leads to a net accumulation of inorganic or available nitrogen in soil water solution (Bartholomew, 1965). This has been attributed to mineralization of organic nitrogen during the decomposition process and its release into water solution. Addition of fertilizer sometimes also leads to the acceleration of decomposition (Harmsen and Kolenbrander, 1965). The decomposition rate of organic matter also seems to change as different substrates are added to it (e.g. Carpenter, 1981).

7.5 MECHANISTIC MODEL OF MINERALIZATION-IMMOBILIZATION PHENOMENA

To attempt to present a unified picture of these various aspects of decomposition, mathematical models have been developed, including a model by Parnas (1975). The basic idea in Parnas' model is that the decomposition rate is limited by the growth rate of decomposers. Decomposers require nutrients. Thus, their growth rate depends on nutrients available in the decaying litter and nutrient in inorganic solute form in the water. Parnas' model is purely one of the decomposition process. Decomposers are present, but the model stops short of describing their mortality and addition to the detrital biomass. Here we describe Parnas' model and its properties to see what controls mineralization and immobilization and to see how these are related to other components of the food web.

In Parnas's (1975) model detritus or organic matter, assumed to be largely plant residue, is divided into two parts: a part consisting of carbon–nitrogen,

or C–N, compounds, such as protein and RNA, and a part termed C compounds, such as cellulose and starch. Detritus is then described by three variables for the standing stocks of carbon and nutrient (nitrogen in this model) in some unit area or volume.

C_1 = amount of carbon in C–N compounds;

N_1 = amount of nitrogen in C–N compounds;

C_2 = amount of carbon in C compounds.

The total detrital carbon in this area or volume is

$$C = C_1 + C_2$$

and C_1 and N_1 are assumed to occur in the C–N compounds in the fixed ratio β.

Decomposers use carbon both for the formation of structure and for providing energy. Not all carbon decomposed from detritus is assimilated into decomposer biomass. Some is released as CO_2. Define:

F = ratio of the carbon assimilated into decomposers to the total amount of carbon released from detritus by decomposers,

f_c = average fraction of carbon in the decomposer's cells,

f_n = average fraction of nitrogen in the decomposer's cells.

These definitions, plus the assumption that nitrogen is used only as structural material, imply that the ratio of carbon to nitrogen used in the formation of decomposer biomass is α/f_n, where $\alpha = f_c/F$; that is, α is the total carbon used by the decomposer organisms per unit decomposer biomass increment.

The task now is to derive equations for the changes in the carbon and nitrogen in the detritus, C_1, N_1, C_2, and the available inorganic nutrient in the area or volume, which is largely ammonium and will be represented by the variable NH_4^+ here. General equations can be written for C and N_1 that apply under all circumstances. The rate of loss of total carbon, C, from the detritus is

$$dD/dt = -\alpha GB \tag{7.1}$$

where

G = specific growth rate of decomposers, which is limited both by N and C, and

B = current biomass of decomposers.

Evidence that the decomposition rate is proportional to decomposer biomass is shown in Figure 7.3. The decomposer growth rate G is a function of total levels of carbon and nitrogen available. Parnas (1975) assumes a multiplicative Monod-type growth function (see O'Neill *et al.*, 1989, for information on this generalization of the Monod function) for this growth

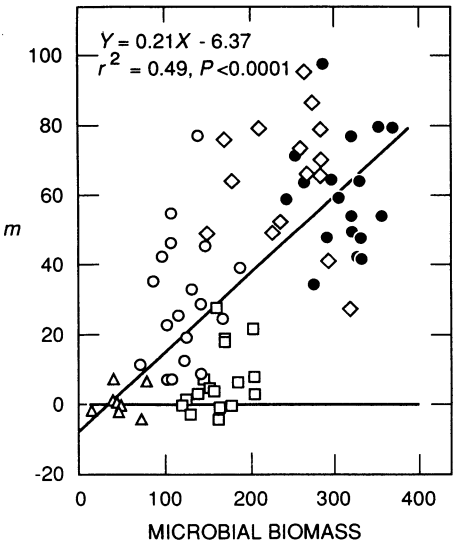

Figure 7.3 Net nitrogen mineralization, m, ($\mu g\ g^{-1}\ 20\,d^{-1}$) as a function of soil microbial biomass (mg of C per 100 g of dry soil) in soils of five sites (denoted by the different symbols) in the Serengeti grasslands. The negative values imply net nutrient immobilization. (From Ruess and McNaughton, 1987.)

rate:

$$G = G_{max}CN/[(k_c + C)(k_n + N)] \tag{7.2}$$

where

G_{max} = maximal growth rate, given high availability of carbon and nitrogen substrate

$N = N_1 + [NH_4^+]$

k_c, k_n = saturation constants for carbon and nitrogen.

Define further

i = immobilization rate, or net rate at which NH_4^+ in solution is taken up by microbial biomass

m = mineralization rate, or net rate of release of NH_4^+ during decomposition

One aspect of the net rate of change of nitrogen, N_1, in the detritus, is the loss due to the rate of nitrogen being taken up by the decomposer, $(f_n GB - i)$. Note that the loss from detritus of nitrogen taken up by the decomposers is offset somewhat if the decomposer obtains some of its needed nutrient directly from inorganic nitrogen in the water solution in the form of an immobilization rate, i. There is also a loss representing the amount of nitrogen mineralized per unit time, m. The equation for the rate

of change of detrital nitrogen is thus

$$dN_1/dt = -(f_n GB - i) - m \tag{7.3}$$

This is a very general equation that is specified in more detail when i and m are determined more specifically.

The rate of nutrient immobilization, i, depends on the amount of inorganic nitrogen present, NH_4^+, compared with nitrogen in the detritus, N_1. The assumption made by Parnas (1975) is that

$$i = f_n GB[NH_4^+]/([NH_4^+] + N_1) \tag{7.4}$$

so that if $[NH_4^+] \ll N_1$ virtually all nitrogen used by decomposers comes from detritus. In the opposite limit $[NH_4^+] \gg N_1$, there is no utilization of detrital nitrogen by the decomposers, since, in that limit it can be seen that the difference between the total uptake of nitrogen and the rate of uptake of nitrogen from water, or immobilization, is very small:

$$f_n GB - f_n GB[NH_4^+]/([NH_4^+] + N_1) \ll f_n GB \tag{7.5}$$

The remaining question is how the decomposers partition their usage of C_1 and C_2. There are two situations in which the decomposers can find themselves with respect to the resources provided by the detritus. First, they can be limited by nitrogen, when the ratio of carbon to nitrogen in detrital biomass is greater than the ratio of nitrogen used to carbon used in forming decomposer biomass, that is, when $C/N_1 > \alpha/f_n$. Second, they can be limited by carbon when the opposite inequality holds, that is, when $C/N_1 < \alpha/f_n$.

In the first case, the rates at which C_1 and C_2 are removed from detrital biomass will be set by the decomposers attempting to maximize the uptake of the limiting nutrient, nitrogen. This would include utilization of NH_4^+ from solution. Thus, the loss rate of nitrogen from detritus is

$$dN_1/dt = -(f_n GB - i) \qquad (C/N_1 > \alpha/f_n) \tag{7.6a}$$

where the immobilization offsets some of the loss from the C–N compounds in the litter. There is no mineralization, m, because all N taken from the litter is used for the growth of the decomposers. The loss of C_1 will be proportional to this by the factor of β, defined earlier as the ratio of C_1 to N_1 in C–N compounds:

$$dC_1/dt = -\beta(f_n GB - i) \qquad (C/N_1 > \alpha/f_n) \tag{7.6b}$$

Finally, the rate of loss of the remainder of the carbon from the detritus used to maintain the growth rate GB [Equation (7.1)] is

$$dC_2/dt = -[\alpha GB - \beta(f_n GB - i)] \qquad (C/N_1 > \alpha/f) \tag{7.6c}$$

The ratio of removal of C_1 to C_2 can range from much greater than 1.0 to much less than 1.0. When the amount of available NH_4^+ is very large, $i \lesssim f_n GB$, and most of the carbon removed is C_2. At the other extreme, when $[NH_4^+]$ is very small, $i \ll f_n GB$, the carbon removed from C–N

compounds, C_1, will play a much larger relative role, as the decomposer will be using C–N compounds preferentially over C compounds in order to obtain nitrogen. Two conclusions were derived by Parnas (1975) from these results:

Conclusion 1: The C/N_1 ratio of organic material being decomposed in the absence of other nitrogen sources will increase with time if its initial C/N_1 is higher than α/f_n, and will not change with time if its C/N_1 is equal to or lower than α/f_n.

Conclusion 2: Where the initial C/N_1 ratio in D is greater than α/f_n, the ratio can decrease with time only if other sources of N are present.

The balances of carbon and nitrogen for $C/N_1 > \alpha/f_n$ are displayed in Figures 7.4(*a*) and 7.4(*b*) respectively. In Figure 7.4(*b*), because nitrogen in detritus is limiting, the fluxes are determined by maximization of nitrogen uptake. Both uptake of NH_4^+ and utilization of N from C–N compounds in

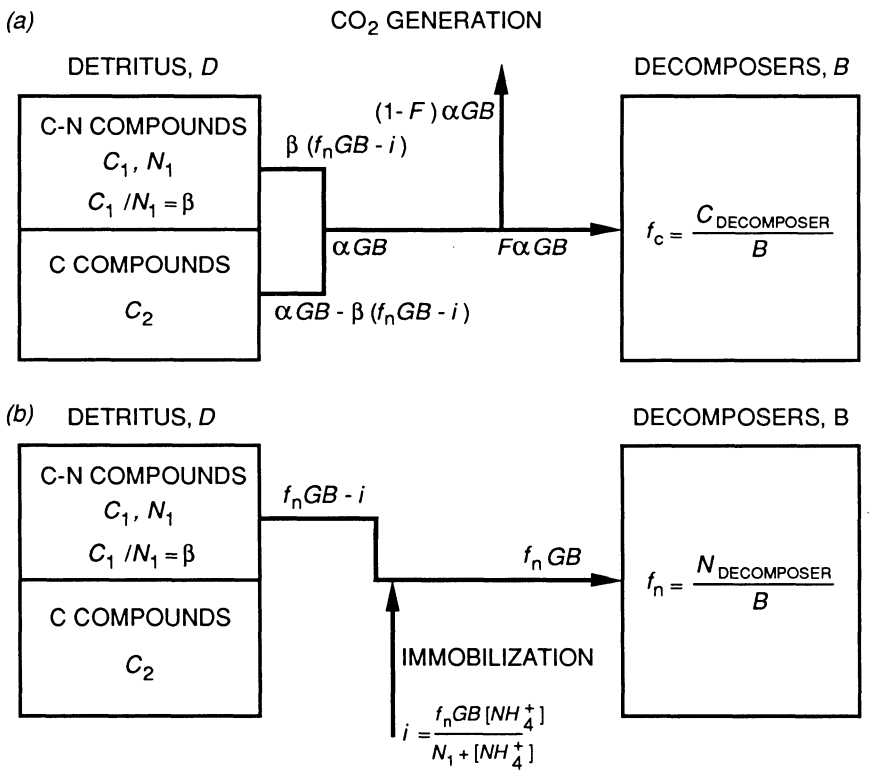

Figure 7.4 Fluxes from detritus to decomposers of (*a*) carbon and (*b*) nitrogen in Parnas' (1976) model, when nitrogen is limiting to decomposers. There is an immobilization rate, i, of NH_4^+ from the solute. $C_{\text{decomposer}}$ and $N_{\text{decomposer}}$ are the amounts of carbon and nitrogen in the decomposers.

the detritus will be used to obtain a total flux of nitrogen, $f_n GB$, to the decomposers. This fixes the flux of carbon from the C–N compounds as $\beta(f_n GB - i)$ (Figure 7.4*a*). The carbon flux from the C compounds in the detritus makes up the difference.

In the second case, when carbon is limiting ($C/N_1 < \alpha/f_n$), the decomposition rate, αGB, is assumed divided between the two fractions in the detritus;

$$dC_1/dt = -\alpha GBC_1/C \qquad (C/N_1 < \alpha/f_n) \tag{7.7a}$$

$$dC_2/dt = -\alpha GBC_2/C \qquad (C/N_1 < \alpha/f_n) \tag{7.7b}$$

Now N_1 is removed from the detrital biomass in proportion to C_1, or

$$dN_1/dt = -\alpha GBN_1/C \qquad (C/N_1 < \alpha/f_n) \tag{7.7c}$$

The decomposer is using the C–N compounds foremost as a carbon source and not all of the nitrogen removed in the process is used. The excess nitrogen may be mineralized. Figure 7.5(a,b) shows the fluxes of carbon and nitrogen between the detritus and decomposers in this case.

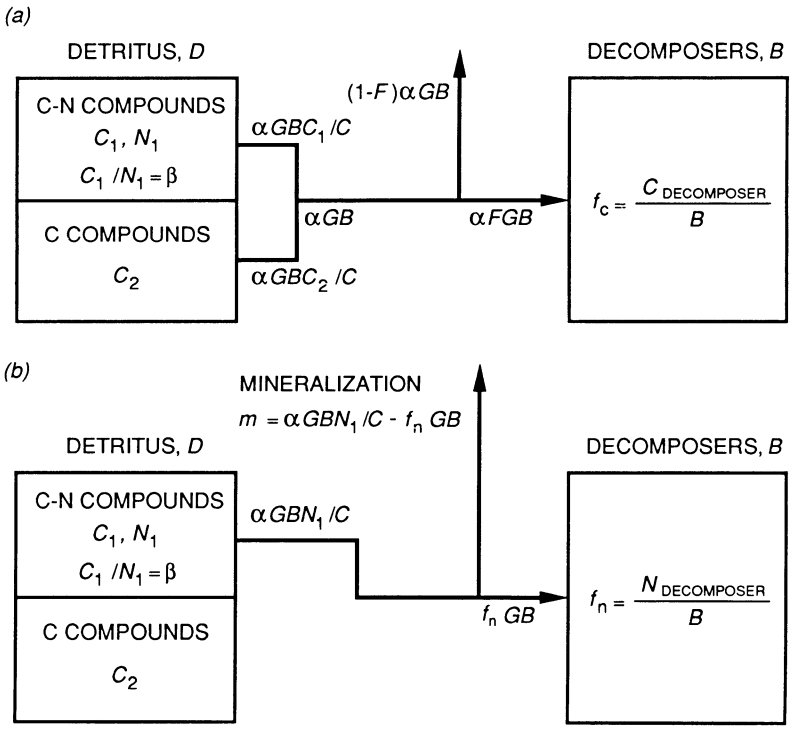

Figure 7.5 Fluxes of (*a*) carbon and (*b*) nitrogen in Parnas' (1975) model, when carbon is limiting to decomposers. There is a net mineralization rate, *m*, of nitrogen.

It is now possible to compute the instantaneous rate of mineralization m as a function of the key variables of the system. By using the general and always valid Equation (7.3), an expression can be derived for m;

$$m = -(f_n GB - i) - dN_1/dt \tag{7.8}$$

When carbon is limiting ($C/N_1 < \alpha/f_n$), dN_1/dt is given by Equation (7.7c) and the immobilization rate $i = 0$. Then, the mineralization rate is

$$m = GB[(\alpha/C)N_1 - f_n] \tag{7.9}$$

Parnas (1975) drew the following conclusions:

Conclusion 3: Mineralization occurs when the C/N_1 ratio for D being decomposed is smaller than α/f_n.

Conclusion 4: The rate of mineralization is increased as C/N_1 is decreased.

Conclusion 5: The higher the amount of NH_4^+ in the area, the higher will be the rate of mineralization.

This rate of mineralization can now be calculated numerically for various values of N_1, C_1, C_2 and $[NH_4^+]$, using Equation (7.9) plus Equation (7.2). Parnas (1975) determined numerical values for parameters of the model as part of a larger model for the US International Biological Programme's Desert Biome (Table 7.2). For these parameters, m is calculated as a function

Table 7.2 Parameter values for a model of decomposition of organic matter by decomposers (from Parnas, 1975)

Parameter	*Meaning*	*Value*
G_{max}	Maximal growth rate of a mixture of decomposers	$0.01\ d^{-1}$
k_c	Constant in Michaelis–Menten term that is the concentration of carbon for half the maximum growth rate of the decomposer	$20\ g\ m^{-2}$
k_n	Constant in Michaelis–Menten term that is the concentration of nitrogen for half the maximum growth rate of the decomposer	$0.4\ g\ m^{-2}$
F	Efficiency of carbon assimilation	0.4
f_c	Fraction of carbon in microbial biomass	0.5
f_n	Fraction of nitrogen in microbial biomass	0.05
β	Molecular ratio between carbon and nitrogen in protein	4.0

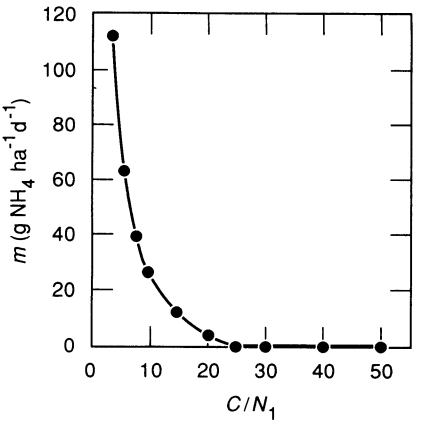

Figure 7.6 Mineralization rate, m, as a function of the C/N_1 ratio in detritus based on parameter values from Table 7.2. (From Parnas, 1975.)

of C/N_1 (Figure 7.6). Below a ratio of $C/N_1 = \alpha/f_n = 25$, mineralization occurs and grows exponentially as C/N_1 decreases.

Parnas (1975) model agrees well with experimental results. For example, in experiments in which organic matter decays and the only nitrogen is that in the C–N compounds in the organic matter, the C/N_1 ratio tends to increase with time (Brown and Dickey, 1970). This finding is predicted by the model, because the C–N compounds are used at a faster rate (proportional to β) than the C compounds (rate proportional to $\alpha - \beta f_n$). When there is additional available nitrogen, then the C/N_1 ratio can decrease due to nitrogen immobilization. The model also supports the experimental finding that when the decaying organic matter is very rich in nitrogen, mineralization will occur. Addition of NH_4^+ will increase the rate of mineralization (Broadbent and Nakashima, 1971).

The equations derived above for the decomposition of detritus do not represent a complete description of the system, since there are no terms for the production of new detritus, no terms for the loss of biomass of the decomposers back to detritus, and no equations for the available nutrient pool or the trophic levels in the ecosystem. In order to provide a description of the effects of decomposition on food web properties, the decomposition model must be integrated into a more complete model of the system. I will not attempt to complete the description of a basic ecosystem here, but will note that such a description must include an equation for available nutrient.

$$d[NH_4^+]/dt = I_n - r_n[NH_4^+] + m - i - F_{NX} \tag{7.10}$$

where an external input, I_n, and a loss, $r_n[NH_4^+]$, have been included and the last term, F_{NX}, represents nutrient uptake by the autotroph, an equation for autotroph biomass, X, an equation for decomposer biomass, B, and equations for C_1, C_2 and N_1. The equations for X and B must reflect the

fact that when there is net immobilization of available nutrients (i.e. when $i > m$) the decomposers and autotrophs compete for nutrients. The autotroph uptake term, F_{NX}, and the immobilization rate, i, must take into account competition between the decomposers and autotrophs for nutrient uptake.

7.6 EFFECTS OF HIGHER TROPHIC LEVELS IN THE DETRITAL FOOD CHAIN

The early concepts of decomposition and recycling of nutrients pictured a system in which bacteria directly released mineralized nutrients into the available pool. However, as discussed above, bacteria may also immobilize nutrients under some circumstances. It has frequently been noted that herbivorous grazing on the bacteria either speeds up the mineralization of nutrients or may even be necessary for net mineralization to occur.

Johannes (1965, 1968) showed in aquatic and marine systems that regeneration of inorganic phosphate from organic detritus proceeded faster when both bacteria and ciliates (which feed on bacteria) are present than when only bacteria are present. Bacteria tended primarily to immobilize nutrients. Barsdate *et al.* (1974) used aquatic microcosms and showed that phosphorus cycled much more rapidly in systems with bacteria and protozoan grazers than with bacteria alone. They hypothesized that the turnover rate of phosphorus in grazed bacteria was higher than that of ungrazed bacteria.

Buechler and Dillon (1974) studied phosphorus turnover by *Paramecia*, which graze on bacteria. They found that bacteria are efficient in removing P from media. They tend not to release it. *Paramecia* feed voraciously on bacteria and excrete most of it. This may account for the release of large amounts of P back into the available pool. Gallepp (1979) noted, in sediment–water microcosms, that chironomids appear to increase the concentration of P in the water above sediments. Chironomids are filter feeders and they release P in faeces.

Cole *et al.* (1978) made similar studies on terrestrial microcosms, simulating rhizospheres with combinations of bacteria, amoeba and nematode populations. Bacteria alone immobilized much of the P from the detritus. Because of the high consumption rate and relatively low assimilation rate of the grazers, amoebae mineralized much of the bacterial P, returning it to an available inorganic pool. At a higher trophic level, nematodes decreased inorganic P, possibly because it limited amoebae.

Anderson *et al.* (1983) carried out a series of microcosm experiments with leaf litter and soil organic matter from deciduous woodlands. Different levels of soil grazing on fungal biomass by macrofauna (e.g. millipedes) were added for a period of 12 weeks and levels of NH_4^+N and NO_3^-N were measured in the soil. Addition of grazers resulted in reduction in nutrient immobilization in litter and soil organic matter.

Douce and Webb (1978) modelled the indirect effects of soil invertebrates on litter decomposition. One effect of soil invertebrates is to graze bacteria (microflora) down to the level where they are growing exponentially. This shortens turnover times. Analogously, Schaeffer and Whitford (1981) proposed that higher trophic levels release nutrients stored by termites. Ants, lizards and birds feed on termites and return nutrients to surface soil.

Ingham *et al.* (1985) proposed a conceptual model for the flows of nutrients (nitrogen and phosphorus) in the decomposer web (Figure 7.7). Note that in this system not only bacterial, but also fungal, decomposition is represented, along with grazers (nematodes) feeding on each. In a set of experimental studies, Ingham *et al.* started with sterile soil and added various components of the decomposer web to see how various combinations affected nutrient mineralization and, hence, plant growth rate. In particular, they tested the hypothesis that nematodes feeding on fungi or bacteria increased the amount of inorganic nutrients available for plant uptake. [This concept is very similar to the effect of herbivores on nutrient levels examined in Chapter 5 (Figure 5.5), where herbivory controlled the autotroph component, which allowed available nutrients to build up.]

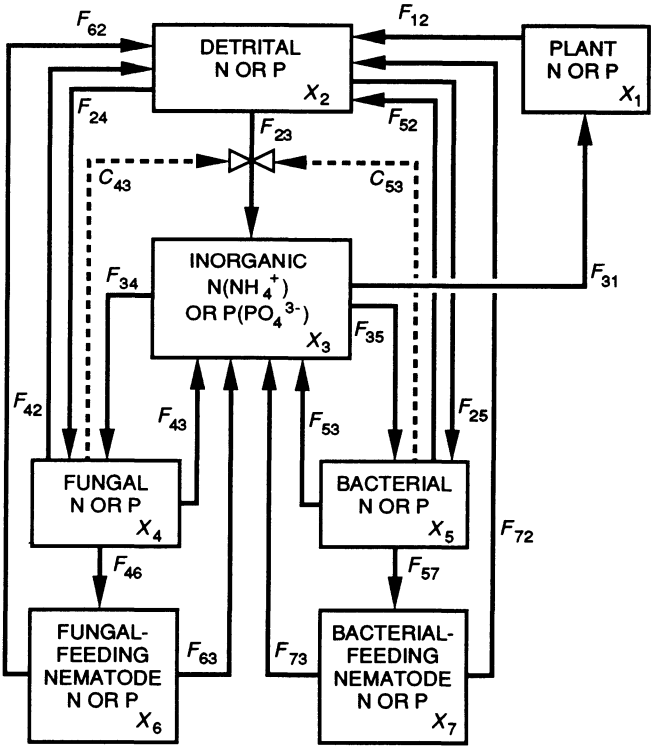

Figure 7.7 Conceptual model of the nutrient flows in a plant plus decomposer system. (From Ingham *et al.*, 1985.)

Ingham *et al.* (1985) found in one set of studies that autotroph production (shoot growth) was higher with bacterial-feeding nematodes than with bacteria alone. Interestingly, bacterial numbers were also higher in the treatment with nematodes than without. The authors proposed a few hypotheses for the apparent stimulatory effect of nematodes on bacteria, including non-lethal passage of many bacteria through nematode guts, where they are exposed to high nutrient levels. This possibility is analogous to the stimulations of autotroph growth by herbivores discussed in Chapter 5.

The interactions of larger grazers with decomposers have even more mutualistic overtones. Ruess and McNaughton (1987) examined nutrient dynamics in different areas of the Serengeti grasslands that are exposed to different levels of ungulate grazing: tallgrass (low grazing), midgrass (moderate grazing) and shortgrass (high grazing) sites. They found that microbial biomass was positively related to the grazing rate. As Figure 7.3 shows, the net rate of mineralization, m, is positively related to microbial biomass, and, as well, is inversely related to the C/N_1 ratio:

$$m = 0.19B - 3.19(C/N_1) + 40.48 \qquad (r^2 = 0.55,\ P < 0.0001) \tag{7.11}$$

Both microbial biomass and mineralization were higher on highly grazed sites. Hence grazing appears to increase soil microbial activity and mineralization in the same sense as it does net primary production and plant net nutrient flux (Ruess *et al.* 1983; Ruess, 1984; McNaughton and Chapin, 1985). The dung from grazers has readily available nutrients and carbon. In some sense the interaction can be thought of as a mutualistic one, since the vertebrate rumens provide an ideal environment for microbes.

Another example of symbiosis is that between fungus-growing ants and some species of saprophytic fungi. The ants cut live leaf parts, prepare them in a variety of ways and place them in fungus gardens. The fungi degrade the plant structural carbohydrates and provide the ants with available nutrients and energy (Swift *et al.*, 1979).

Visser (1986) reviewing the influences of soil invertebrates on microbes, mentioned three main effects:

1. Comminution, or mixing and channelling of litter and soil.
2. Grazing on the microflora.
3. Dispersal of microbial propagules.

Of these, comminution has traditionally been felt to be the most important in speeding nutrient recycling, through 'exposing a greater surface area to microbial attack' (Satchell, 1974). This may not be the case for all soil invertebrates, however. Hassall *et al.* (1987) were unable to substantiate that comminution of leaf litter enhanced microbial metabolism. They suggested instead that the foraging of isopods on leaf litter on the surface at night and transporting the material as faeces to moist resting sites may accelerate soil microbe use of the material.

7.7 SUMMARY AND CONCLUSIONS

The dead organic matter or detritus can play an important role in the nutrient dynamics of an ecosystem and, therefore, has implications for system stability. In particular, a large detrital compartment buffers the living components of the system against large fluctuations in nutrient availability. This does not necessarily increase all types of stability, however. For example, we found in Chapter 5 that limitations in nutrient availability generated by herbivore–autotroph cycles tend to counteract those cycles, often stabilizing the system. In the present chapter it was shown that when the system has a large, relatively constant detrital component, these nutrient fluctuations do not occur and herbivore–autotroph oscillations will not be damped by out-of-phase changes in nutrient availability.

In contrast to this possible effect of not hindering autotroph–herbivore oscillations, a detrital component that is large relative to the living components of the system can have a positive effect on resilience of the system to perturbations affecting the living parts of the system. The steady local input of the nutrient from the decomposing detrital compartment enables autotrophs and higher trophic levels to recover more quickly than they would if only external sources of limiting nutrients had to be relied on. It was also shown, however, that a perturbation to the detrital compartment in such a case, as might occur in a stream during a heavy scouring event, could have a drastic effect on the system, as resilience would be very low for such a disturbance.

This chapter has also touched on some of the actual complexity involved in decomposition and nutrient release, which in previous systems was assumed to occur at a rate linearly proportional to detrital compartment size. In fact, detritus is a mixture of compounds with different ratios of nutrients such as nitrogen and phosphorus to carbon. The decomposers that break down detrital matter need nutrients also, and this affects how rapidly they act and whether they immobilize the nutrients released from the detritus in their own biomass or cause a net mineralization of nutrients, which are then available for the autotrophs of the system. The rate of nutrient mineralization is not controlled by the decomposers, bacteria and fungi, alone, but is affected in a variety of ways by soil invertebrates and herbivorous vertebrates.